# Do the gas exchange characteristics of alien acacias enable them to successfully invade the fynbos?

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The invasive success of alien *Acacia* species in the fynbos could be partially attributable to physiological differences to indigenous fynbos. In this investigation we tested the hypothesis that the greater N availability due to the $N_2$-fixing ability of acacias would result in greater Rubisco activity and photosynthetic capacity, relative to fynbos species. The gas exchange characteristics, leaf N concentrations and photosynthetic N use efficiencies of *Acacia saligna* and *Acacia longifolia* were compared with those of *Protea repens*, *Chrysanthemoides monilifera*, *Dodenea viscosa* and *Leucadendron salignum*. Compared to the fynbos species, the acacias had larger leaves and higher leaf water contents, but intermediate specific leaf areas. The acacias had more than 3-fold higher leaf N concentrations, but 50% lower photosynthetic nitrogen use efficiency than the fynbos species. The acacias showed no clear photosynthetic advantage over the fynbos species, although, the former tended to have higher photosynthetic capacities and water use efficiencies. The lack of correlation between leaf N concentrations and photosynthetic capacity or Rubisco activity may have been due to differences in the utilisation of N for nonphotosynthetic processes and in the activation state of Rubisco. It seems unlikely that photosynthetic characteristics play an important role in the invasive success of alien acacias in the Fynbos biome.

**Keywords**: *Acacia*, fynbos, invasive, nitrogen, photosynthesis.

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## Introduction

A striking feature of the Fynbos Biome is the presence, if not dominance, of invasive alien trees and shrubs, especially those of the genera *Acacia*, *Hakea*, and *Pinus* (Richardson *et al.* 1992). Invasion of catchment areas is not only of concern because of its effect on biodiversity, but also due to its effect on water yield (van Wilgen *et al.* 1992, van Wilgen *et al.* 1997, van Wilgen *et al.* 1998). Other ecological effects of aliens on the biome include the alteration of coastal sediment movement patterns, the acceleration of river bank erosion, changes in fire regime, alteration of the composition of soil and changes in plant and animal communities (van Wilgen *et al.* 1997). The reasons for the success of the invasive alien *Acacia* species are complex (Richardson *et al.* 1992), but are partially the consequence of physiological differences which give the acacias a competitive advantage over the fynbos species (Witkowski 1991). The alien acacias have greater above-ground biomass (Kruger 1977) and greater litter production (Witkowski 1991) than indigenous fynbos species. The more profuse growth of the aliens enables them to out-compete the fynbos species.

Factors accounting for the low annual productivity in Mediterranean-type ecosystems have been suggested to include the low volume and seasonality of the water regime and the low availability of soil nutrients, particularly in the Australian and South African regions. Comparisons of the water relations of fynbos plants with those of other Mediterranean-type ecosystems indicated that water is not a major limiting factor in fynbos (Stock *et al.* 1992). The role of nutrients as a selective force promoting convergence has been shown to differ between the relatively nutrient-rich chaparral, matorral, and maquis Mediterranean climate ecosystems and the nutrient-poor systems of Australia and South Africa (Kruger *et al.* 1983). Therefore, any analysis of the distribution of water use optimisation patterns along aridity gradients is complicated in fynbos regions by associated nutrient gradients. Miller (1985) showed that water appears to act as a selective pressure in the fynbos region only on nutrient-rich soils. Thus, the generalisation that moisture availability is the major factor determining vegetation patterns does not hold for the Fynbos Biome (Stock *et al.* 1992). In a study of *Acacia melanoxylon*, Brodribb and Hill (1993) suggested that increased internal carboxylation resistance or enzymatic inhibition limits photosynthesis in water stressed foliage. A comparison between true leaves and phyllodes in this species showed that phyllodes appeared to be better adapted to conditions of water stress and high light intensity, resulting in a higher maximum photosynthetic rate per unit area than found in true leaves. The light requirements of Mediterranean climate species have been related to their low N concentrations which do not allow for high photosynthetic capacities (Mooney *et al.* 1983). Studies of plant responses to nutrient additions (Witkowski *et al.* 1990), litter decomposition processes (Mitchell *et al.* 1986), and N allocation patterns (Stock *et al.* 1987) indicate that nutrient-poor soils impose limitations on plant growth and development. N fertilisation of *Protea lepidocarpodendron* resulted in increased photosynthetic rates (Stock *et al.* 1992) which supports the hypothesis that low leaf N contents probably constrain the photosynthetic capacity of fynbos species. Nutrient-poor systems such as fynbos are often C-rich, and C produced in excess by a plant can be used for storage or the production of fire resistant structures (e.g. Proteaceae). C-rich sclerephyllous leaves are a striking feature of fynbos and may be an adaptation to improve nutrient use efficiency because sclerophylly entails an increased C return per unit of nutrient invested. Photosynthetic gas exchange studies show photosynthetic rates of fynbos to be generally low, similar to those measured in several Mediterranean climate sclerophyllous shrubs (Stock *et al.* 1992).

Factors such as soil pH, salinity, water relations and exposure to wind probably interact with P availability together with biotic factors to determine the distribution of the acacias (Witkowski, 1994). Witkowski (1991) studied the effects of invasive acacias on nutrient cycling and found that the N status of the fynbos ecosystems is elevated by the invasion by alien acacias, given that they produce more litter, with three times the N content of that of the indigenous species. Similarly, Stock *et al.* (1995) observed

decreases in soil C:N ratios which were attributed to inputs from *Acacia* species. These authors regarded the $N_2$-fixation process as crucial for the success of the invaders and emphasised that nutrient enrichment and nutrient mineralisation patterns could persist long after the acacias have been removed, which could severely restrict the re-establishment of indigenous species.

Mycorrhizal infection occurs in relatively few fynbos species and generally to a small extent (Allsopp & Stock 1993a, b). Part of the competitive advantage acacias have over fynbos species may lie in their ability to form extensive symbiotic associations with arbuscular mycorrhizal fungi which are thought to enhance host water relations, mineral nutrition and growth, particularly under stressed environmental conditions, such as the nutrient-poor soils of the western Cape. Hoffman and Mitchell (1986) showed that *Acacia saligna* have a more extensive root system, greater abundance of root nodules and greater mycorrhizal infection than indigenous Fabaceae species.

$N_2$-fixation by acacias results in greater N availability for protein synthesis and may increase Rubisco levels in comparison to indigenous fynbos species. Rubisco activity is an important limiting factor for photosynthesis (Evans 1990). The acacias should thus exhibit greater photosynthetic capacity which in turn would provide C for growth, fixation of $N_2$ and mycorrhizal development. Furthermore, greater photosynthate availability in acacias may result in extensive root development and allow better access to water. In addition, the transpiration rates of the acacias may be lower than in similar fynbos plants because of the greater Rubisco activity and consequently the possibility exists that smaller stomatal conductance will be required for similar photosynthetic rates. In this study the photosynthetic gas exchange characteristics of the phyllode bearing *Acacia saligna* and *Acacia longifolia* were compared with the indigenous *Protea repens*, *Chrysanthemoides monilifera*, *Dodenea viscosa* and *Leucadendron salignum* in an attempt to explain some of the competitive advantages of the alien acacias over the fynbos species. $A:C_i$ curves were constructed to determine photosynthetic capacities and the activity of Rubisco and leaf total N concentrations were determined to allow calculation of the photosynthetic N use efficiencies (PNUE).

*Abbreviations*

$A_{(0)}$, photosynthetic assimilation rate (in the absence of stomatal limitation); $C_a$, atmospheric $CO_2$ concentration; $C_i$, intercellular $CO_2$ concentration; $J_{max}$, substrate supply limited assimilation; *l*, stomatal limitation of assimilation; SLA, specific leaf area; $V_{Rubisco}$, velocity of RuBP carboxylation; PNUE, photosynthetic nitrogen use efficiency; Rubisco, RuBP carboxylase/oxygenase; WUE, water use efficiency.

## Materials and Methods

### Site description

The study was undertaken during August and September 1998 on the northern slopes of Stellenbosch Mountain, south east of Stellenbosch. The study site was an area of *c.* 0.3 km$^2$ between 140 and 240 m above sea level. The aspect of the site was predominantly northerly and exposed. The site had been subjected to disturbance in the past. The geology comprises Cape Granite underlying Quartsite Sandstone of the Table Mountain Group with a deep substrate, mainly consisting of gravel and clay. The soil is well leached and relatively poor in nutrients due to the high mean annual rainfall of 800 mm. The climate is typically Mediterranean with winter rains and very dry summers during which temperatures reach 36°C. The mean annual temperature is 16.4°C (Lötter & van Wageningen 1988).

### Gas exchange determinations

A Ciras I infra red gas analyser (PP Systems, Hitchin, Herts, UK) with a light and temperature controlled Parkinson PLC broad leaf cuvette was used to measure photosynthetic assimilation rate (A), water use efficiency (WUE), and intercellular $CO_2$ ($C_i$) of the leaves and phyllodes, henceforth termed 'leaves'. Leaves in the middle region of the new season's growth were selected as being representative of the assimilation rates after gas exchange analysis of five age-classes of leaves of each species indicated no strong trend of gas exchange characteristics with age (data no shown). The response of A to $C_i$ ($A:C_i$) was measured at light intensities previously determined to be saturating (PAR *c.* 1800 µmol m$^{-2}$ s$^{-1}$) and at *c.* 20°C by varying the external $CO_2$ concentration from 0 to *c.* 2 000 µmol mol$^{-1}$ and the data was expressed on the basis of either leaf area or dry weight. One equation was used to fit the data expressed on the basis of leaf area ($A = a - be^{-cCi}$, Cramer & Richards 1999) and another was used for the data expressed on the basis of leaf DW ($A = \frac{aCib}{aCi + b} - c$, Olsson & Leverenz 1994). Two different equations were used after extensive testing because these were found to be empirically better suited to the particular data sets. The portion of the curve where the slope approaches zero due to limitation in the supply of substrate (RuBP), termed $J_{max}$ (Lawlor 1987), was calculated from these equations. Linear regression was performed on the data between a $C_i$ of 0 and 200 µmol mol$^{-1}$ $CO_2$ to determine the efficiency of carboxylation ($V_{Rubisco}$; Lawlor 1987). The relative stomatal limitation (*l*) was calculated from $l = (A_0 - A)/A_0$ where A is the assimilation rate measured at 360 µmol mol$^{-1}$ $CO_2$ and $A_0$ is the rate in the absence of stomatal limitations, i.e. A interpolated from the response curve at $C_i$ = 360 µmol mol$^{-1}$. The photosynthetic leaf areas were determined by using a leaf area meter (Licor, USA).

### Total N digestion

Leaves were collected from different positions from the current season's growth and leaf areas measured using a Licor leaf area meter. Fresh leaves were weighed, oven dried (80°C), weighed again and the specific leaf areas (SLA, m$^2$ kg$^{-1}$) calculated. The dried leaf material was milled in a Wiley mill (A.H. Thomas, Philadelphia, PA) using a 60 mesh screen and *c.* 0.03 g material digested in 35 cm long tubes with a Kjeldahl tablet (Merck, Germany) and 3 ml 3.4% (w/v) salicylic acid in 13.5 M sulphuric acid. The samples were digested at room temperature for 2 h, 200°C for 1 h, 270°C for 1 h and 370°C for 1 h. The digest was made up to 50 ml with distilled water and assayed for $NH^{4+}$ using a modification of the method of Solorzano (1969). Sub-samples of 50 µl were added to 12.5 ml 0.12% EDTA (w/v), 1 ml phenolic nitroprusside [1:1 mixture of 10% (w/v) phenol in 95% ethanol and 0.5% (w/v) sodium nitroprusside] and 1.25 ml alkaline hypochlorite (0.075 M $NaH_2PO_4$, 0.51 M NaOH and 0.7% sodium hypochlorite). The samples were allowed to stand for 1 h and the absorbance measured at 635 nm.

### Statistical analysis

Replication of measurements was through sampling different individual plants. Where analysis of variance was performed, post-hoc Fisher's protected least significant difference (LSD) tests were conducted to determine the significance ($P < 0.05$) of differences between the species using Statgraphics Ver. 7.0 (1993). In the tables, different letters have been used to indicate significant differences between species.

## Results

### Plant characterisation

*A. saligna* and *P. repens* had large leaves relative to the other fynbos species (Table 1). The two *Acacia* species had higher water contents than the fynbos species, except for *C. monilifera*

**Table 1** Comparison of the leaf fresh weight (FW), leaf dry weight (DW), leaf water content and specific leaf area (SLA) of alien (*A. saligna* and *A. longifolia*) and indigenous plants (*P. repens, C. monilifera, D. viscosa* and *L. salignum*). The means ± SE (n = 6) are followed by letters indicating whether the treatments had a significant ($P < 0.05$) influence as determined by one-way ANOVA followed by Fisher's protected LSD multiple range tests

| Species | FW g | DW g | Water g $H_2O$ $g^{-1}$ DW | SLA $m^2$ $kg^{-1}$ |
|---|---|---|---|---|
| *A. saligna* | 1.53 ± 0.12 f | 0.52 ± 0.04 e | 2.0 ± 0.1 d | 6.4 ± 0.2 c |
| *A. longifolia* | 0.47 ± 0.04 d | 0.17 ± 0.02 c | 1.8 ± 0.1 c | 7.3 ± 0.3 d |
| *P. repens* | 0.63 ± 0.03 e | 0.32 ± 0.01 d | 1.0 ± 0.0 a | 3.0 ± 0.2 a |
| *C. monilifera* | 0.40 ± 0.03 c | 0.09 ± 0.01 b | 3.5 ± 0.1 e | 10.7 ± 0.2 f |
| *D. viscosa* | 0.12 ± 0.01 b | 0.05 ± 0.00 ab | 1.3 ± 0.1 b | 8.0 ± 0.3 e |
| *L. salignum* | 0.08 ± 0.01 a | 0.04 ± 0.00 a | 1.1 ± 0.0 a | 4.9 ± 0.2 b |

which had the highest water content of the species examined. The remaining fynbos species exhibited fairly uniform values. The SLA (Table 1; Figure 1) of *C. monilifera* was the highest, while the two *Acacia* species did not show particularly high SLA values. Therefore, the alien and fynbos species cannot be separated on the basis of SLA as all the species are significantly different from each other.

### Total leaf N contents, WUE and PNUE

There was a significantly greater N concentration per leaf area of the two alien species than of the fynbos species, with *P. repens* being intermediate between the two groups (Table 2). When the N concentration was expressed per gram of dry weight, the aliens and fynbos species formed two distinct groups with the acacias having 3.5-fold higher leaf N concentrations than the fynbos species. The photosynthetic assimilation rates expressed per gram DW (Table 2) of the fynbos species were generally low, except for *C. monilifera*. The high photosynthetic rate of *C. monilifera* was related to its high SLA (Table 1). The fynbos species were more photosynthetically efficient in their N use than the *Acacia* species (PNUE, Table 2), although the PNUE of *P. repens* was intermediate between the fynbos and acacia groups. There were also no clear differences in WUE between the acacia and fynbos species, although, *A. longifolia* had the highest WUE of the species examined (Table 2).

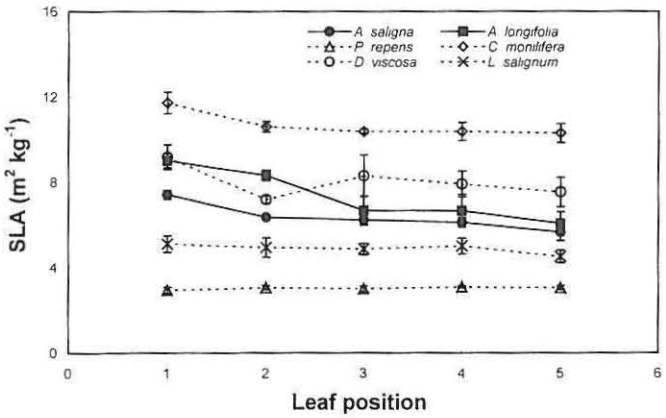


**Figure 1** The specific leaf area (SLA) at different leaf positions of alien (*A. saligna* and *A. longifolia*) and indigenous (*P. repens, C. monilifera, D. viscosa* and *L. salignum*) plants. Leaf position 1 = youngest fully expanded leaf and 5 = oldest leaf of the new season's growth.

### Photosynthetic capacity and efficiency

In this investigation a simple empirical approach (Olsson & Leverenz 1994; Cramer & Richards 1999) was used to obtain the parameters of the A:$C_i$ curves, rather than the more complex mechanistic approach detailed by Harley *et al.* (1992) thus avoiding assumptions and complex parameter estimation. However, the two approaches yielded similar $V_{Rubisco}$ and $J_{max}$ values. Although the acacias had high photosynthetic capacities, there was no clear difference between the acacias and the fynbos species (Figure 2). All the species showed high values of $C_i$ at an ambient $CO_2$ concentration of 360 µmol $mol^{-1}$ ($C_i@C_a$ = 360, Table 3) compared to those of tomato plants (Cramer & Richards 1999), indicating that the photosynthetic rates of all the species were similarly limited by the stomata and carboxylation resistance. The photosynthetic rate (A, Table 3) of *A. saligna* was high, while *D. viscosa* and *L. salignum* had very low photosynthetic rates. The photosynthetic rates in the absence of stomatal limitation ($A_0$) exhibited the same trend. However, there was no clear separation between the acacia and fynbos groups with respect to either A or $A_0$ whether assimilation was expressed per unit of leaf area or per unit of leaf dry weight (Figure 2). The stomatal limitations ($l$) were also similar in all the species. The $J_{max}$ values tended to be low in the fynbos and higher in the acacias, although there is no clearly significant difference between the two groups. Both the $J_{max}$ and the $V_{Rubisco}$ data exhibited an asymptotic relationship with the leaf total N (Figure 3). $J_{max}$ was at its maximum above a total N concentration of *c.* 100 mmol N $m^{-2}$ and the corresponding value for $V_{Rubisco}$ was *c.* 50 mmol N $m^{-2}$. *A. saligna*, *A. longifolia* and *P. repens* had high leaf N concentrations and high photosynthetic capacities compared to *C. monilifera, D. viscosa* and *L. salignum*. Although *A. saligna* had a very high leaf N concentration, its $J_{max}$ was not distinctly different from that of the other species. The respiration rates of *D. viscosa* and *L. salignum* were particularly high.

## Discussion

*P. repens*, and to a lesser extent *C. monilifera*, were the only indigenous species comparable to the acacias in their growth form, being relatively tall woody shrubs, while the other two fynbos species were considerably smaller. The physiological comparison was, therefore, between considerably different life forms,

**Table 2** Leaf total N, expressed per leaf area and per gram of leaf dry weight; photosynthetic assimilation rate measured at Ca = 360 µmol mol-1 (A) expressed per gram of dry weight; water use efficiency (WUE) and photosynthetic nitrogen use efficiency (PNUE) of alien (*A. saligna* and *A. longifolia*) and indigenous plants (*P. repens, C. minolifera, D. viscosa* and *L. salignum*). The means ± SE (n = 6) are followed by letters indicating whether the treatments had a significant ($P < 0.05$) influence as determined by one-way ANOVA followed by Fisher's protected LSD multiple range tests

| Species | Total N mmol $m^{-2}$ | Total N mmol $g^{-1}$ DW | A nmol $g^{-1}$ DW $s^{-1}$ | WUE mmol $mol^{-1}$ | PNUE µmol $mol^{-1}$ $s^{-1}$ |
|---|---|---|---|---|---|
| *A. saligna* | 150 ± 32 c | 0.95 ± 0.19 b | 127 ± 1 c | 3.9 ± 0.4 bc | 149 ± 28 a |
| *A. longifolia* | 98 ± 11 b | 0.71 ± 0.07 b | 140 ± 7 d | 4.8 ± 0.4 c | 204 ± 28 ab |
| *P. repens* | 57 ± 12 ab | 0.17 ± 0.04 a | 37 ± 1 a | 4.0 ± 0.6 bc | 241 ± 41 abc |
| *C. monilifera* | 27 ± 3 a | 0.29 ± 0.03 a | 182 ± 3 e | 3.7 ± 0.5 b | 646 ± 75 c |
| *D. viscosa* | 45 ± 6 a | 0.36 ± 0.04 a | 101 ± 3 a | 4.1 ± 0.7 bc | 302 ± 49 bc |
| *L. salignum* | 27 ± 3 a | 0.13 ± 0.02 a | 43 ± 3 b | 1.8 ± 0.2 a | 341 ± 34 d |

but the selected species were nevertheless representative of the invaded fynbos and acacia groups. The alien acacias tended to have larger leaves and higher water contents than the fynbos species. This may be due to better access to water through symbiotic AM associations (Allsopp & Stock 1993) or lower transpiration rates than in the indigenous fynbos. Although the WUE of the acacias was relatively high, there was no clear difference between the acacia and fynbos species. Thus, the detrimental effects of alien acacias on water runoff into catchments (van Wilgen *et al.* 1997) is not due to inefficiency of water use by the acacias, but rather due to the large above-ground biomass and dense stands of these plants.

Differences in the SLA between the species were similar throughout the different leaf age classes (Figure 1). According to Poorter (1990), van der Werf (1996) and Hunt and Cornelissen (1997), SLA is one of the major factors controlling growth across a wide range of species and fast-growing species tend to have a higher SLA than slow-growing ones. However, our data does not support this conclusion as no significant differences were found between the SLA of the acacia and fynbos groups. The high light intensities experienced in the western Cape, as opposed to the lower light intensities used in studies by van der Werf (1996) and Hunt and Cornelissen (1997), may account for the difference between our results and the findings of these authors. In a low-light intensity environment reduced respiratory costs associated with high SLA's could be more important in maintaining a positive balance between photosynthesis and respiration, whereas in the C-rich (Stock *et al.* 1992) light-sufficient fynbos, nutritional status is likely to be more important in determining growth rates. Furthermore, the correlation between SLA

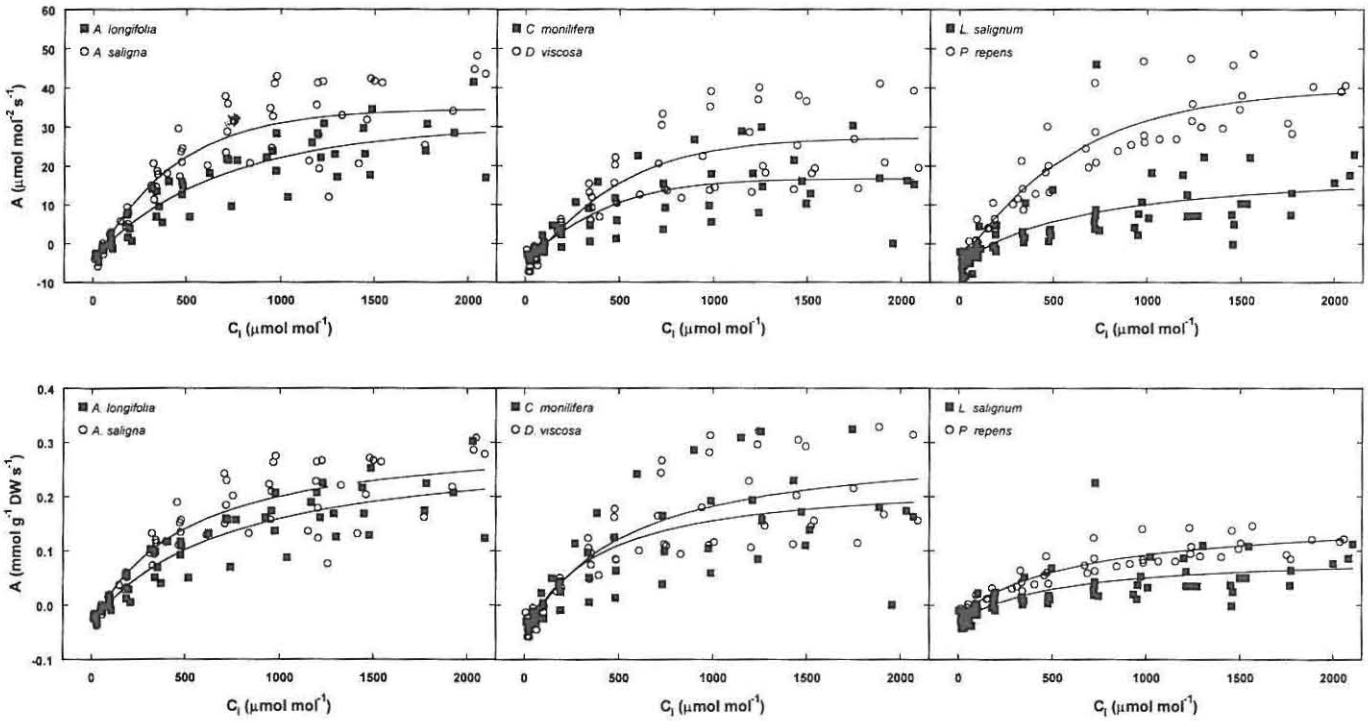


**Figure 2** The response of photosynthetic assimilation rate (A) to intercellular $CO_2$ concentrations ($C_i$), expressed per unit of leaf area and per unit of leaf dry weight, of alien invasives (*A. saligna* and *A. longifolia*) and indigenous fynbos species (*P. repens, C. monilifera, D. viscosa* and *L. salignum*). Experimental conditions as for Table 3.

**Table 3** Comparison of variables from A:$C_i$ curves expressed per unit leaf area between alien (*A. saligna* and *A. longifolia*) and indigenous plants (*P. repens, C. monilifera, D. viscosa* and *L. salignum*): $C_i$ at $CO_2$ concentration of 360 µmol $mol^{-1}$ ($C_i@C_a$ = 360); photosynthetic assimilation (A); photosynthetic assimilation in the absence of stomatal limitation ($A_0$); stomatal limitation of assimilation ($l$); substrate supply limited assimilation ($J_{max}$); velocity of RuBP carboxylation ($V_{Rubisco}$); and respiration rate. Measurements were performed at a saturating light intensity of 2 000 µmol $m^{-2}$ $s^{-1}$ between 11:00 and 17:00. The cuvette air temperature and humidity were regulated at 20°C and 10 mBar, respectively. The means ± SE (n = 6) are followed by letters indicating whether the treatments had a significant ($P < 0.05$) influence as determined by one-way ANOVA followed by Fisher's protected LSD multiple range tests

| Species | $C_i@C_a$ = 360 µmol $mol^{-1}$ | A µmol $m^{-2}$ $s^{-1}$ | $A_0$ µmol $m^{-2}$ $s^{-1}$ | $l$ | $J_{max}$ µmol $m^{-2}$ $s^{-1}$ | $V_{Rubisco}$ mol $m^{-2}$ $s^{-1}$ | Respiration µmol $m^{-2}$ $s^{-1}$ |
|---|---|---|---|---|---|---|---|
| *A. saligna* | 339 ± 1 a | 17 ± 1 c | 18 ± 1 c | 0.062 ± 0.009 a | 35 ± 5 b | 0.063 ± 0.006 a | 4.5 ± 0.7 a |
| *A. longifolia* | 342 ± 3 ab | 12 ± 3 bc | 13 ± 3 bc | 0.054 ± 0.006 a | 33 ± 5 b | 0.055 ± 0.014 a | 4.4 ± 0.6 a |
| *P. repens* | 342 ± 1 ab | 14 ± 2 bc | 15 ± 2 bc | 0.056 ± 0.005 a | 39 ± 3 b | 0.065 ± 0.005 a | 5.2 ± 1 0.8 ab |
| *C. monilifera* | 341 ± 2 ab | 13 ± 3 bc | 14 ± 3 bc | 0.057 ± 0.005 a | 28 ± 4 ab | 0.052 ± 0.006 a | 3.9 ± 0.4 a |
| *D. viscosa* | 345 ± 1 b | 10 ± 2 b | 11 ± 2 b | 0.053 ± 0.004 a | 27 ± 5 ab | 0.059 ± 0.008 a | 7.1 ± 0.9 bc |
| *L. salignum* | 351 ± 1 c | 3.3 ± 1.7 a | 3.5 ± 1.7 a | 0.066 ± 0.013 a | 19 ± 4 a | 0.040 ± 0.012 a | 7.6 ± 0.8 c |

and growth rate obtained by van der Werf (1996) and Hunt and Cornelissen (1997) pertains to optimal N supply, while the Fynbos Biome is generally regarded to have N deficient soils and the fynbos species have particularly low total leaf N (Table 2).

The photosynthetic rates of the acacia species were high relative to the other fynbos species, but the differences between the acacia and fynbos species were not large when expressed either on the basis of leaf dry mass or area (Tables 2,3; Figure 2).

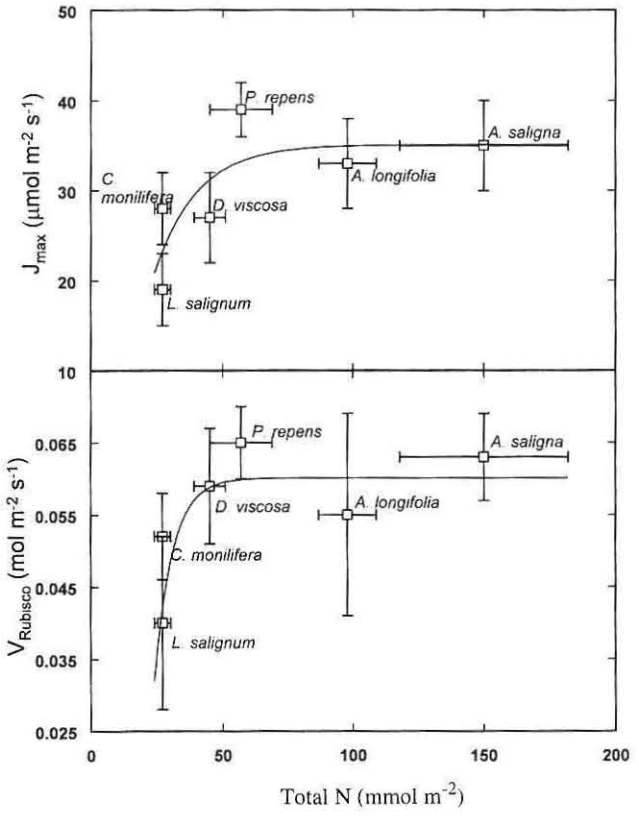


**Figure 3** The relationship between leaf total N concentration and the photosynthetic capacity ($J_{max}$) and carboxylation efficiency ($V_{Rubisco}$) of alien (*A. saligna* and *A. longifolia*) and indigenous plants (*P. repens, C. monilifera, D. viscosa* and *L. salignum*). Values represent the mean and bars the SE (n = 6).

Poorter (1990) reported photosynthetic rates varying between 130 and 330 µmol $g^{-1}$ $s^{-1}$ for eight species varying in relative growth rates between 136 and 268 mg $g^{-1}$ $d^{-1}$. In comparison to these values, both the acacia and the fynbos species exhibited low photosynthetic rates, although, the rates obtained for the fynbos species in this study were in the range of those found for other fynbos species as reviewed by Stock *et al.* (1992). The leaf N concentration (Table 2) of the acacias were in the range of those reported by Poorter (1990) for the eight species, but the leaf N concentrations of fynbos species were considerably lower than the lowest value (*c.* 100 mmol N $m^{-2}$) reported by this author. The relatively high photosynthetic rates and low N concentrations combined to result in very high PNUE's in comparison to those reported by Poorter (1991) for the eight species which ranged between 34 and 82 µmol $mol^{-1}$ $s^{-1}$, indicating the low N status of the fynbos species and their ability to overcome this restriction on photosynthesis.

The high leaf N concentrations of the two *Acacia* species and their low PNUE relative to the fynbos species indicated that these plants use a large proportion of their N for processes other than photosynthesis. A similar conclusion may be reached from the curvilinear relationship between $J_{max}$ and $V_{Rubisco}$ with leaf total N (Figure 4). A substantial amount of the N in the acacias may be invested in non-photosynthetic compounds and structures, as concluded by Pons (1990) for plants with high leaf N. Feedback inhibition of photosynthesis due to low sink activity may also influence PNUE (van der Werf 1996). The situation in the fynbos group is different from the acacia group, because the fynbos species had relatively low leaf N concentrations and high PNUE. The fynbos species clearly have a different strategy of N and C utilisation. The small amount of N that is available is used efficiently for photosynthetic purposes, while C, which is abundant, is invested into structures such as schlerophyllous leaves. Schlerophylly may, therefore, be an adaptation improving nutrient use efficiency because it entails an increased carbon return per unit of nutrient invested (Stock *et al.* 1992) due to longer leaf area duration, as well as being an adaptation to drought.

The $V_{Rubisco}$ of all the species were similar despite the significant difference between the aliens and the fynbos in their leaf total N (Tables 2 & 3). The $V_{Rubisco}$ for both the acacia and fynbos species were low relative to those obtained for tomato plants (Cramer & Richards 1999) indicating relatively low carboxy-

lation efficiencies. As the $V_{Rubisco}$ is weakly correlated with the leaf total N, our results imply that there could be differences in the activation state of Rubisco. According to Evans (1983) a decrease in nitrogen supply leads to a decrease in Rubisco content and an increase in the activation state of Rubisco. In addition, factors such as sink limitation, P limitation and down-regulation of Rubisco may possibly account for the relatively low Rubisco activity in the acacias, found in this investigation.

Given their high leaf N, it was also expected that the photosynthetic capacities ($J_{max}$) of the acacias would be considerably higher than those of the fynbos species. The $J_{max}$ values were of similar magnitude to those obtained for tomato plants (Cramer & Richards 1999). Although a trend towards higher photosynthetic capacities in the acacias can be seen from the $J_{max}$ values (Table 3), the results did not clearly support the expectation that the acacias would have significantly greater $J_{max}$ values than the fynbos species. It is remarkable that the $J_{max}$ of *P. repens* was higher than that of *A. saligna* and *A. longifolia* with relatively little leaf total N. *P. repens* also had a high photosynthetic rate per leaf area (Table 3), but due to its low SLA it had a low photosynthetic rate per gram of DW (Table 2). Van der Heyden and Lewis (1989) have previously distinguished proteoid species in the fynbos as having comparatively high photosynthetic rates. *P. repens* probably invests a large proportion of available photosynthate into respiration to maintain the greater leaf biomass per unit leaf area. The high photosynthetic rate of *C. monilifera*, when expressed per unit of leaf dry weight, is related to its high SLA and high leaf water content. The particularly high respiration rates of *D. viscosa* and *L. salignum* (Table 3) may also contribute to slow growth.

A large degree of variability in the photosynthetic rates was observed (Figure 2). This is to be expected from sampling natural populations and has been found by other investigators (Stock pers. com.). Variation in environmental conditions may contribute to the variability in photosynthetic rates. In this regard, measuring plants of different ages, on different days, at different times of the day, and possibly slightly different soils, may all influence the results. Although the leaf chamber used regulates the conditions of the section of leaf measured, this provides only very localised constant conditions. The edaphic and environmental conditions that the rest of the plant experiences would have an effect on the photosynthetic rate. Similarly, the physiological status of the whole plant, e.g. sink metabolism, will influence the photosynthetic performance.

## Conclusion

The data showed no clear photosynthetic advantage of the *Acacia* species over fynbos species, although the former tended to have high photosynthetic rates and capacities. Therefore, the reason for the more rapid growth of the alien invaders has to be related to other factors such as water use efficiency, N and P status, respiratory factors, or a combination of these and relatively high photosynthetic rates with other ecological factors.

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